

A REVISION OF OCHROBRYUM (LEUCOBRYACEAE)

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DEDICATION

Not so long ago I began to learn moss taxonomy with a copy of Howard Crum's *Mosses of the Great Lakes Forest*, a gift from Ronald Pursell. My continued interest in mosses, to a great extent, is due to my beginning with that special book. I am, therefore, especially grateful to be able to contribute the following paper to this Festschrift honoring Howard Crum.

INTRODUCTION

Ochrobryum was established by Mitten (1869) for two leucobryaceous mosses with short, immersed capsules. The genus has a bizarre sporophytic complex that is unique in the Leucobryaceae: a short seta, a hemispherical, eperistomate capsule, and a short, symmetrical, rostrate operculum tightly enclosed by an exceedingly long (to three times the length of the operculum), narrowly subulate, mitrate calyptra. In form the capsule and the operculum are so similar that the former has been described as "an inverted operculum . . ." (Robinson 1990). The calyptra, which may or may not be fringed at base by long unicellular hairs, is generally longer than the combined operculum, capsule and seta. At capsule dehiscence the operculum commonly remains inside the calyptra. The resulting operculum/calyptra complex, although longer, has the same form as the deoperculate sporophyte.

The leaves of *Ochrobryum* have the alternating leucocyst/chlorocyst arrangement typical for the Leucobryaceae. Unlike many members of the family the leaves at base are nearly always three layered: one dorsal leucocyst layer, a central chlorocyst layer and one ventral leucocyst layer. Occasionally, the unistratose pattern in the dorsal layer is disrupted by the subdivision of one or two dorsal leucocysts. But, this is a non-typical event and leaves that are three-layered at base represent an essential feature of *Ochrobryum*. Three-layered leaves are also found in a few *Leucobryum* species, and in the neotropics *Ochrobryum* is frequently misidentified as *L. martianum* (Hornsch.) Hampe, a three-layered leaf species that otherwise has little resemblance to *Ochrobryum*.

In general, *Ochrobryum* leaves have ventral leucocysts positioned opposite the dorsal leucocysts. As a result the chlorocysts are four-sided. The chlorocysts proximally are isocentric, i.e., as close to the dorsal surface as to the ventral surface. However, as noted by Cardot (1900), the chlorocysts distally are hypocentric, i.e., closer to the dorsal surface than to the ventral surface. This hypocentric chlorocyst pattern is caused in two ways: all *Ochrobryum* species have enlarged upper ventral leucocysts, and in some species the upper ventral leucocysts are multilayered. The degree of chlorocyst hypocentricity is greater in these latter species than in the species with only enlarged leucocysts. Commonly, the species with multilayered

upper ventral leucocysts have fleshy or swollen leaf apices that are obtusely triangular in cross-section.

In past treatments of *Ochrobryum* leaf apex form has been used as a primary taxonomic character at the species level. This character, though useful, is astoundingly variable within single collections of some species. Consequently, it is best regarded as a secondary taxonomic character. The greatest variability in apical leaf form is found in those species that have multilayered upper ventral leucocysts (*O. gardneri* (C. Müll.) Mitt. and *O. kurzianum* Hampe in Besch.). In these species most leaves have fleshy, broadly acute to obtuse leaf apices. However, nearly all collections have some sharply acute leaves. Commonly, in these species the lower leaves are sharply to broadly acute while the upper leaves are fleshy and obtuse. For the species having only enlarged upper ventral leucocysts or a multi-layered pattern for only a single cell width (*O. subulatum* Hampe in Besch., *O. sakalavum* Card. & Par., and *O. sessile* Allen) the leaf apices are generally more sharply acute (obtuse in *O. sakalavum*) and not fleshy or swollen. Since all species of *Ochrobryum* have at least a few leaves with some type of acute apex, the use of leaf apical form as a distinguishing feature must always be accompanied by subjective qualifiers such as "most" or "some".

An interesting and characteristic feature of the leaves in *Ochrobryum* is the appearance of the upper chlorocysts. Distally the chlorocysts are short, and form chains of rounded to quadrate cells. This feature is well-developed in all *Ochrobryum* species and its presence is of critical importance in recognizing the genus when sporophytes are absent. Unfortunately, the feature is not unique to *Ochrobryum*; Cardot (1900) noted it in a number of *Leucobryum* species and considered the Leucobryaceae to commonly have chlorocysts that are wider toward the apex than toward the base. In this regard it should be noted that *Leucobryum incurvifolium* C. Müll. (one of the few *Leucobryum* species with erect capsules) has this chlorocyst feature as equally well-developed as any species of *Ochrobryum*.

Globose, budlike propagula were not attributed to *Ochrobryum* until 1901 (Geheeb 1901). Robinson (1990) considered these propagula to be a feature that uniquely defined the genus within the Leucobryaceae. All species in the genus, except *O. sakalavum* which is known only from a scanty type collection, possess propagula of this type. Generally the propagula end in a single blunt cell, however some species have propagula that end in a sharp cell. But, even in these latter species a few propagula with blunt terminal cells can also be found. The globose propagula are attached at their proximal ends to a central, reddish-brown stalk of variable length by an elongated cell. The position at which the propagula occur on the plant is a character of primary taxonomic significance at the species level. The propagula may be borne on the upper dorsal surface of the leaves, in globose masses at the end of a specialized, apical stalk, or clustered in the leaf axils.

Although *Ochrobryum* is largely defined by its sporophytic complex, the complex within the genus is nearly uniform. The only character in the complex that varies greatly is the degree and type of fringing of the calyptral base. In three species, *O. subulatum* (Asia, South America, Africa), *O. kurzianum* (Asia), and *O. sakalavum* (Madagascar) the base of the calyptra is densely beset with long, single-celled fringe cells. In the other species, *O. gardneri* (Central and South America, Africa) and *O. sessile* (Central and South America), the calyptra base may be weakly fringed or simply laciniate. In *O. gardneri* both fringed and laciniate calyptrae can be observed in the same collection.

Long, single-celled, fringed calyptrae are widely and sporadically found within

the Dicranaceae, Leucobryaceae, Hookeriaceae and Daltoniaceae. The unsuitability of this character as an indicator of natural relationships outside of a generic context is obvious from the fact that the calyptral fringe cells of *Ochrobryum* are identical in morphology and position to those found scattered in many genera in these families. Even the variable nature of the calyptral fringing in *Ochrobryum* has a counterpart in some species of *Campylopus* where fringed and un-fringed calyptrae can be found within single collections. Robinson (1990) considered fringed calyptrae in the Leucobryaceae (*Schistomitrium* and *Ochrobryum*) to be a localized apomorphy because of its sporadic occurrence within the family.

The erect capsules and mitrate calyptrae of *Ochrobryum* have led to the view that the genus is closely related to *Schistomitrium* (Mitten 1859, Andrews 1947). Further gametophytic support for this view is found in the hypocentric upper chlorocysts of *Ochrobryum*. As noted above, some species of *Ochrobryum* have leaf apices with enlarged, multilayered leucocysts. These leaf apices are essentially identical to the leaf apices found in species of *Schistomitrium* where this type of leaf apex represents a generic feature.

Robinson (1990) considered the generic subgroup of *Schistomitrium*, *Cladopodanthus* and *Holomitriopsis* to be the only Leucobryaceae-subgroup marked by more than one synapomorphy—mitrate calyptrae, hypocentric chlorocysts, and erect capsules. *Ochrobryum* has all three of these character states and clearly belongs within the complex. Indeed it appears better placed there than *Holomitriopsis* which has a cucullate calyptra. Robinson (1990) did not include *Ochrobryum* in the complex because of its unusual sporophyte and its globose vegetative propagula. As treated here these features are considered indicators of generic rather than subfamilial rank.

Ochrobryum was revised by Bescherelle (1897). This revision added fourteen species and one variety to the genus, many of which were sporophytically unknown. Cardot (1900) considered *Ochrobryum* and *Leucobryum* gametophytically inseparable and so transferred or excluded Bescherelle's species known only from gametophytic material. Cardot recognized nine species of *Ochrobryum* distributed in southern Asia and South America. Subsequently, the genus has been discovered in Central America and Africa. Wijk *et al.* (1964) attributed 20 taxa to the genus. Robinson (1965) added another species, but since he also transferred a Sri Lankan species of *Ochrobryum* to *Leucobryum*, 20 species are currently recognized in the genus.

TAXONOMIC TREATMENT

Ochrobryum Mitt., J. Linn. Soc., Bot 12: 107. 1869.—TYPE: *Leucophanes gardneri* C. Müll., Bot. Zeit. 2: 741. 1844.

Plants small, 3–20 mm high, pale-green to whitish. Stems red to reddish-brown, erect, simple or sparingly branched, commonly with numerous arrested branch primordia along all sides; in cross-section cells thin- to firm-walled, epidermis undifferentiated, central strand absent. Rhizoids of two types: stout, smooth, sparsely and irregularly branched, dark red to red-brown ones distributed on all sides of the stems at base; and slender, smooth to lightly roughened, at times pinnately branched, pale reddish-brown ones on stems above and below leaf insertions and at times from the dorsal sides of the leaf apices. Pseudoparaphyllia absent. Paraphyllia

absent. Leaves erect-incurved, erect-spreading to flexuose, channeled; margins entire; lamina narrow, restricted to the lower half of the leaf; in cross-section at base with a median row of quadrate chlorocysts and single layers of dorsal and ventral leucocysts, at leaf apex chlorocysts hypocentric, and having one or several layers of enlarged ventral leucocysts; chlorocysts short in the upper region of the leaf, forming chains of rounded or quadrate cells; alar cells not differentiated. Axillary hairs delicate, 4-6 cells: basal cell short rectangular, hyaline to gray, upper cells long rectangular, hyaline, terminal cells rounded at the apex. Asexual reproduction by means of globose propagula clustered on short stalks: 1) on dorsal surface of leaf towards the apex, 2) on apex of specialized terminal branch or stem extension, 3) in leaf axils, and 4) on slender rhizoids at base of stems. Dioicous. Perigonia terminal on short branches at apex of stem. Perichaetia terminal on stem, archegonia 800 μ m long, with slender, elongate neck 550 μ m long. Setae short, smooth, vaginula well developed; capsules immersed to shortly exerted, hemispheric to obconic, wide-mouthed when dry; annulus non-revolvible, consisting of several rows of thick-walled irregularly shaped cells at operculum and capsule mouth and two rows of long rectangular, yellowish, thin-walled cells at site of separation; stomata absent; opercula long-rostrate; peristome absent. Calyptra long-rostrate, the rostrum more than twice the operculum length, mitrate (occasionally splitting irregularly and appearing cucullate), lacinate or ciliate-fringed at base.

Etymology. A combination of the Greek *ochros* (pale, sallow, pale-yellow) and *bryon* (moss).

Distribution. CENTRAL AMERICA: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. SOUTH AMERICA: Colombia, Venezuela, Brazil, and Bolivia. AFRICA: Guinea, Zaire, and Madagascar. ASIA: India, Nepal, Burma, Thailand, Cambodia, and Malaysia.

KEY TO THE SPECIES OF *OCHROBRYUM*

1. Leaves linear to setaceous, gradually narrowed from base to apex; apices mostly sharply acute, usually a few apices broadly acute 2.
1. Leaves lanceolate, narrowly ovate at base; apices broadly acute or obtuse, both types in same collection 3.
 2. Propagula clustered in leaf axils; apical ventral leucocysts frequently two-layered in the middle for a single cell width 4. *O. sessile*.
 2. Propagula clustered at tip of propaguliferous branch or stem extension which has reduced leaves; apical ventral leucocysts in a single layer 5. *O. subulatum*.
3. Leaves with apical ventral leucocysts two-layered in the middle for a single cell width; leaf lamina narrow at base, 2-4 cells wide 3. *O. sakalavum*.
3. Leaves with apical ventral leucocysts bi- to multi-layered in a broad band; leaf lamina broad at base, 4-10 cells wide 4.
 4. Propagula on upper, dorsal leaf surface; basal leaf laminae with 4-6 layers of long-rectangular cells; plants of the neotropics and Africa 1. *O. gardneri*.
 4. Propagula clustered in leaf axils; basal leaf laminae with 6-10 layers of long-rectangular cells; plants of Asia 2. *O. kurzianum*.

1. *Ochrobryum gardneri* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 108. 1869, "gardnerianum" see nomenclatural note 1. *Leucophanes gardneri* C. Müll., Bot.

Zeit. 2: 741. 1844. *Schistomitrium gardnerianum* (C. Müll.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 26. 1859. TYPE. BRAZIL. *Gardner 94* (BM, H, NY isotypes).

Leucophanes gardnerianum C. Müll., Syn. Musc. Frond. 1: 85. 1849, *ortho. var.*

Leucobryum obtusifolium C. Müll., Bot. Zeit. 15: 577. 1857. *Schistomitrium obtusifolium* (C. Müll.) C. Müll., Ann. Sci. Nat. Bot., Sér. 5, 3: 339. 1865.

Ochrobryum obtusifolium (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 108. 1869. TYPE. COLOMBIA. Santa Martha, Minca, *Funck & Schlim in coll. Linden 913* (BM, BR, H, NY isotypes), *syn. nov.*

Ochrobryum phyllanthum Lindb. in Besch., J. Bot. (Morot) 11: 141. 1897, *nom. nud. in synonym.* Based on BRAZIL, environs de Caldas, juillet 1854, *Lindberg* (BM).

Ochrobryum paulense Broth. & Geh. in Geh., Rev. Bryol. 28: 11. 1901. TYPE. BRAZIL. São Paulo: near Apiaby, *Puiggari 561* (H isotype), *syn. nov.*

Ochrobryum normandii Card. & Par. in Par., Rev. Bryol. 29: 65. 1902. TYPES. GUINEA. Fouta Djallon: près Donhol Neera, 29 mars; entre Dango & Bouna, 30 mars; Bourrougal Tope, 2 avril; près riv. Kaligourou, 29 avril; all collected in 1901 by *Normand* (types not seen, see nomenclatural note 2), *syn. nov.*

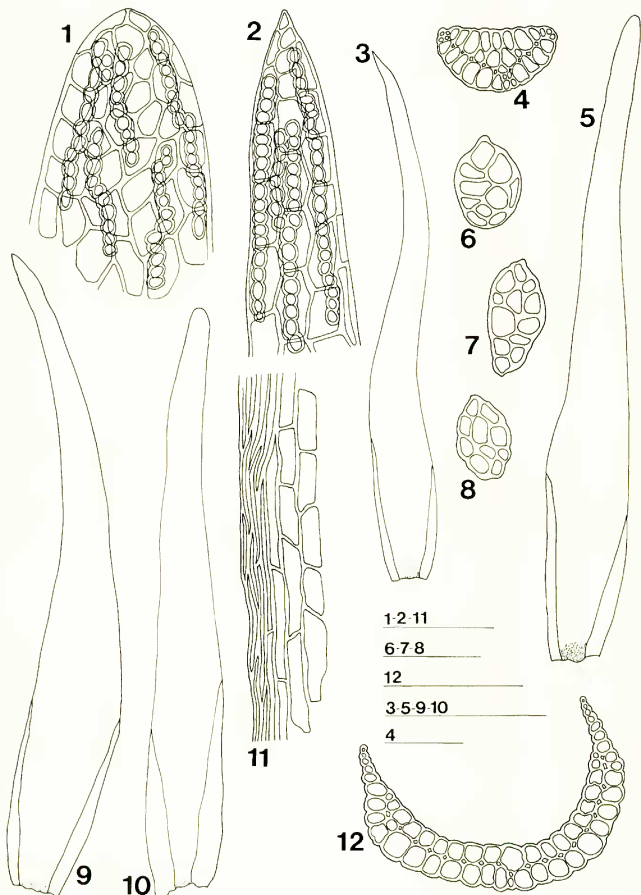
Ochrobryum dendeliae Broth. & Par. in Par., Rev. Bryol. 31: 117. 1904. TYPE. GUINEA. Ad arbores secus amnem Dendeli, 4 mart 1904, *Pobeguïn* (BM, H, NY isotypes), *syn. nov.*

Ochrobryum crumii Robins., Bryologist 68: 92. 1965. TYPES. MEXICO. Jalisco: La Cumbre, 10 mi SW of Autlán, *Crum 1247* (US holotype; F, NY isotypes). PARATYPES. MEXICO. Jalisco, *Crum 438a* (MICH, not seen), *1334* (US), *syn. nov.*

Nomenclatural notes.

1. Wijk *et al.* (1964) incorrectly attributed the combination *O. gardneri* to Lindberg (1872) rather than Mitten (1869). This error can be attributed to Müller's (1849) use of an orthographic variant (*gardnerianum*) for a listing of his previously described *Leucophanes gardneri*. Müller never intended *L. gardnerianum* to be a new species as is evidenced by his direct reference in the species citation to his earlier paper. Mitten (1869) unfortunately used Müller's orthographic variant when transferring the species to *Ochrobryum*. In accordance with Article 75.3 (Greuter 1988) the epithet should be automatically corrected. In fact, it would seem that Lindberg (1872) was not effecting a transfer of the species but simply rectifying an orthographic error as can be seen from his citation of the species: *O. gardneri* (C. Müll.) Mitt.
2. The types of *O. normandii* were not available for study. Nevertheless, it is synonymized with *O. gardneri* on the basis of Cardot's statement (in Paris 1904) that the type of *O. macclaudii* is a mixture of that species (the fertile plants) and *O. normandii* (the sterile plants). My examination of this type material reveals a mixture of *O. subulatum* (fertile plants) and *O. gardneri* (sterile plants).

Plants in compact tufts or cushions, greenish-white, becoming whitish-brown with age. Stems 3–13(–20) mm high. Leaves 2–5 mm long, 0.3–0.8 mm broad, closely and densely erect-patent or stiffly patent-spreading, narrowly ovate-lanceolate to lanceolate, shortly acuminate, bluntly acute or rounded obtuse, at times cucullate, frequently apiculate; margins erect; leaf lamina narrow, consisting of 2–4 rows of long-rectangular, variously porose cells at midleaf and 4–6 rows of rectangular, firm-walled cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; apical ventral leucocysts multi-layered. Asexual reproduction by brown, multicellular, globose propagula



FIGS. 1-12. *Ochrobryum gardneri*. 1 & 2. Leaf apices. 3, 5, 9, 10. Leaves. 4. Leaf cross-section at apex. 6-8. Globose propagula. 11. Basal leaf lamina. 12. Leaf cross-section at base. Scales in mm: 1, 2 & 5 = 0.1; 3 = 0.2; 4 = 1.0. Figs. 1, 2, 4, 8, 11, 12 from *Gardner 94*; figs. 3, 5, 6, from *Crum 1247*; figs. 7, 9, 10 from *Linden 913*.

clustered on short stalks on the upper dorsal leaf surface. Setae smooth, 1.0–1.5 mm long; capsules immersed to emergent, 0.5–1.0 mm long; opercula 1.5 mm long. Calyptrae 4–5 mm long, ciliate or lacinate at base. Spores spherical, smooth or lightly roughened, 12–18 μ m.

Distribution. Central America (Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama); South America (Colombia, Brazil, and Bolivia); Africa (Guinea).

Illustrations. Bescherelle (1897, figs. 1, 5); Cardot (1900, plate 8, fig. 37); Bartram (1949, fig. 31, A–D); Robinson (1965, figs. 15–21); Yano (1975, fig. 28, a–g); Figs. 1–12.

Habitat. On rotting logs or tree trunks, and on bark at base of trees; 105–2200 m.

Specimens examined. CENTRAL AMERICA. MEXICO. Chiapas: above Mapastepec, *Sharp 4409* (US); Colima: Alzada, *Orcutt 5359* (FH); Jalisco: La Cumbre, *Crum 1247* (F, NY, US). GUATEMALA. Alta Verapaz: Cobán, *Tiirckheim* (NY); Baja Verapaz: near Jicaro, *Sharp 2660a* (FH). HONDURAS. Olancho: 14°54'N; 85°56'W. *Olson 83-7b* (MO). NICARAGUA. Jinotega: near Jinotega, *Standley 9566* (F). COSTA RICA. San José: Santa María de Dota, *Standley & Valerio 43142* (FH, NY, US), *Standley 41628* (FH, H, US), *Standley 41651* (FH, US). PANAMA. Chiriquí: 8°35'N. 81°45'W. *Allen 5218* (MO), Santa Clara, *Mori & Bolten 7169* (MO), 2 mi S of Boquete, *Crosby 3961* (MO, PMA), Cerro Pando, 8°52'N, 82°45'W, *Hamilton et al. 811* (MO), 2 mi E of Boquete, *Nee 10804* (MO, NY, PMA, US).

SOUTH AMERICA. COLOMBIA. Magdalena: Santa Marta, *Linden 913* (BM). BRAZIL. Bahia: 11°39'S, 41°07'W, *Vital 8038* (MO); Goiás: Serra Geral do Paran, *Irwin et al. 31982 p.p.* (FH, H, NY), *Irwin et al. 33185* (FH, H, NY), *Irwin 33208a* (NY); Minas Gerais: Caldas, *Mosen* (H), Lagoa Santa, *Warming* (BM); So Paulo: Faxima, *Puiggari 561* (H). BOLIVIA. La Paz: Santa Anna, Apolo region, *Williams 1861* (BM, FH, H, NY); Santa Cruz: Velasco Province, Ro Blanco, *Herzog* (H), Prov. Velasco, 15°58'S, 61°05'W, *Lewis 85-1036* (MO).

AFRICA. GUINEA. Fefin, *Maclaud p.p.* (BM); Lambeira, *Pobegun* (BM, NY); Dombiagn, *Pobegun* (H, NY); Dendeli, *Pobegun* (H); Diendieu, *Pobegun* (NY).

This species and *O. kurzianum* form a close pair marked by the presence of bluntly acute to obtuse leaves that are distinctly swollen or thickened at the extreme apex due to their enlarged and multi-layered upper ventral leucocysts. *Ochrobryum kurzianum* differs in having propagula clustered in the leaf axils and by its better developed leaf laminae (6–10 layers of long rectangular cells). The two species are geographically distinct: *O. gardneri* Central America, South America and Africa; *O. kurzianum* Asia.

The leaf apices in *O. gardneri* are remarkably variable, even within single collections. At times nearly all leaves are obtuse and apiculate, conversely some collections have mostly broadly acute leaves. All collections have leaves with thickened apices and at least some obtuse leaves. Globose propagula borne on the upper dorsal leaf surface are a constant, diagnostic feature of *O. gardneri*.

This species is similar to *O. sessile* which is sympatric with it in Central America and northern South America. *Ochrobryum sessile* has moderately stout leaves with leaf apices that approach those of some plants of *O. gardneri*. In addition, the leaf apices frequently have ventral leucocysts in a two-layered pattern for a single cell width in the middle of the leaf. *Ochrobryum sessile* differs not only by its lack of an extensive apical region of multilayered ventral leucocysts, but also by having propagula clustered in the leaf axils and smoothly tapered, narrower, more sharply acute leaves.

Ochrobryum subulatum frequently occurs mixed with *O. gardneri*. It is a more slender plant with narrowly acute leaves, a constant uni-layered ventral leucocyst

pattern, and has globose leaf propagula on specialized, terminal branches or stem extensions.

Vegetatively this species resembles *Leucobryum polakowskyi* (C. Müll.) Card. or *L. incurvifolium*. But, these two species proximally have multi-layered dorsal and ventral leucocysts, quadrate basal laminal cells, and they reproduce asexually by means of terminal clusters of reduced leaves.

Holomitriopsis laevifolia (Broth.) H. Robins., a Venezuelan species with obtuse, apiculate leaves and a single dorsal and ventral leucocyst-pattern, may also approximate this species. *Holomitriopsis laevifolia* is a more robust plant, lacks rounded to quadrate apical chlorocysts and leaf propagula, has a cucullate calyptra, and a peristomate capsule.

2. *Ochrobryum kurzianum* Hampe in Besch., J. Bot. (Morot) 11: 145. 1897. TYPES.

BURMA. Moulmein, *Stoliczka* [Kurz] 4434 (BM lectotype; BM, BR, H isolectotypes), *Stoliczka* [Kurz] 4438 (BM, H syntypes); Pegu-Yomah, *Kurz* 2890 (BM, H, NY syntypes); Martaban, *Kurz* 2842 (BM, H, NY syntypes).

Ochrobryum kurzianum Hampe in F. Mason, *Burma* 2: 49. 1883, *nom. nud.*

Ochrobryum nepalense Besch., J. Bot. (Morot) 11: 145. 1897. TYPE. NEPAL.

Wallich 30 (BM holotype; BM isotypes), *syn. nov.*

Ochrobryum parishii Besch., J. Bot. (Morot) 11: 142. 1897. TYPE. BURMA.

Moulmein, *Parish* 2 (BM holotype; NY isotype), *syn. nov.*

Nomenclatural notes.

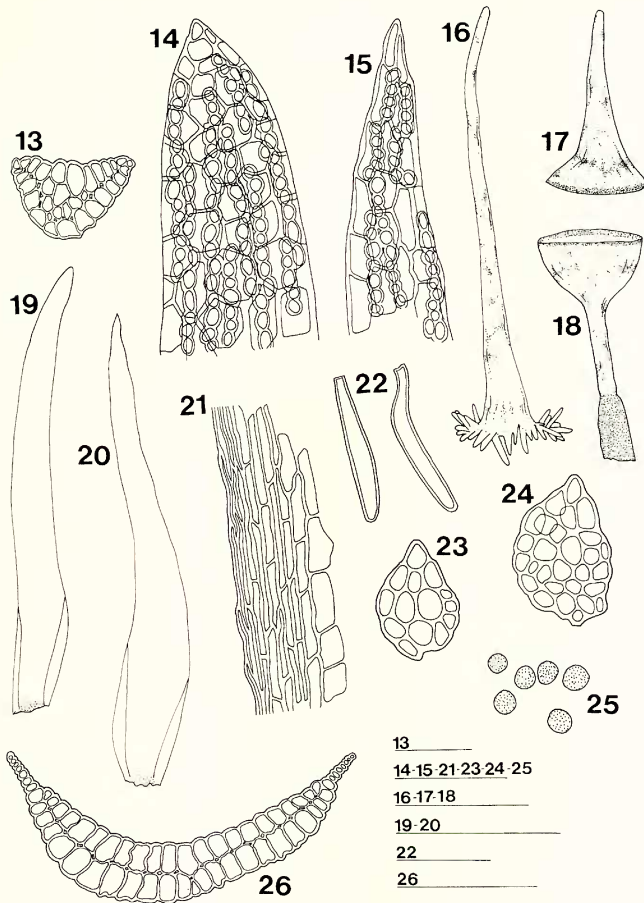
1. The above three species have equal priority. The epithet *kurzianum* is used for the combined taxon since it is the name in common use in Asia.
2. The lectotype of *O. kurzianum* (the only type material in the Bescherelle herbarium) was cited as "*Stoliczka, S. Kurz 4434*" (Bescherelle 1897), but the specimen in Hampe's herbarium was evidently collected solely by Stoliczka. Hampe's specimen has one of Kurz's printed labels on which Stoliczka's name has been hand-written and Kurz's name crossed out.
3. The type of *O. parishii* is *Parish* 2, but specimens at BM and NY with the number 22 may also be type material. The error may have occurred when Mitten (1856) listed *Parish* 2 as "22. *Schistomitrium gardnerianum*"; in the same paper *Parish* 22 is a hepatic. The holotype has no collection number. In the Mitten herbarium there is one specimen of *Parish* 2. All material listed as *No.* 22, *Parish* (BM, NY) is considered possible type material.

Plants in compact tufts or cushions, greenish-white, becoming whitish-brown with age. Stems 5–15 mm high. Leaves 2–4 mm long, 0.5–0.8 mm broad, closely and densely erect-patent or stiffly patent-spreading, narrowly ovate-lanceolate to lanceolate, shortly acuminate, bluntly acute or rounded obtuse; swollen or fleshy at the apex; margins erect; leaf lamina narrow, consisting of 6–8 rows of long-rectangular, variously porose cells at midleaf and 6–10 rows of elongate-rectangular, firm-walled cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; ventral leucocysts multi-layered at the extreme apex. Asexual reproduction by brown, multicellular, globose propagula on very short stalks clustered in the leaf axils. Setae smooth, 1.0–1.7 mm long; capsules immersed to emergent, 0.5–0.75 mm long; opercula 1.0 mm long. Calyptrae 4–5 mm long, strongly ciliate at base. Spores spherical, lightly roughened, 10–17 μm .

Distribution. Asia (India, Nepal, Burma, Thailand, and Cambodia).

Illustrations. Bescherelle (1897, figs. 2, 3, 4); Cardot (1900, plate 8, figs. 39, 40); Gangulee (1969, fig. 193); Eddy (1990, fig. 185); Figs. 13–26.

Habitat. On rotting logs or tree trunks, and soil over rock; 50–1600 m.



FIGS. 13-26. *Ochrobryum kurzianum*. 13. Leaf cross-section at apex. 14 & 15. Leaf apices. 16. Calyptra. 17. Operculum. 18. Capsule, seta and vaginula. 19 & 20. Leaves. 21. Basal leaf lamina. 22. Calyptral hairs. 23 & 24. Globose propagula. 25. Spores. 26. Leaf cross-section at base. Scales in mm: 1 & 2 = 0.1; 3 & 4 = 1.0; 5 & 6 = 0.2. Figs. 13 & 26 from *Touw 9450*; figs. 14-21 from *Kurz 2890*; figs. 22-25 from *Beddome 804*.

Specimens examined. INDIA. Assam: Garo Hills, *Marten 5702* (H, NY); Orissa: Eastern Ghats, Jeypore Talug, *Walker 529, 579* (BM), Russelconda Hills, 19°50'N; 84°35'E, *Beddome 804* (BM, NY). NEPAL. *Wallich 30* (BM). BURMA. Pegu: Pegu-Yomah, *Kurz 2890* (BM, H, NY); Tenasserim: Moulmein, *Parish 2* (BM, NY), *Parish 112* (BM, H), *Stoliczka 4434, 4438* (BM), Martaban, *Kurz 2842* (BM, H, NY). THAILAND. Chanthaburi: Kao Sabah, *Kerr 108* (BM); Kanchanaburi: Ta Kanun, *Kerr 145* (BM); Krabi: Krabi, *Kerr 503* (BM); Payap: 98°35'E, 18°30'N, *Touw 9450* (BM, MO, NY); Trat: Koh Chang, Klong Munsé, *Schmidt 20* (BM, H); Adang: Salut, *Kerr 245* (BM). CAMBODIA. Kandal: near To Bong, *Poilane* (BM, H, NY).

In one paper, Bescherelle (1897) described three *Ochrobryum* species—treated here as one species—based on variations in plant size, leaf apex shape and the number of cell rows in the basal lamina. These distinguishing features are extremely variable and not constantly expressed even within single collections. A nearly identical range of variation is exhibited by *O. gardneri* for the same characters.

Ochrobryum kurzianum and *O. gardneri* were treated by Mitten (1859) as a single species. Bescherelle (1897) separated them on the basis of their allopatric distributions, and the presence in *O. gardneri* of shorter, flatter, narrower, acuminate-acute leaves that had a narrower basal leaf lamina (4 vs. 10 rows of cells). Most of these distinctions are not valid, but these two species do differ in three ways. The basal leaf lamina of *O. gardneri* is generally narrower, its propagula are borne on the upper dorsal surface of the leaves rather than in the leaf axils, and its calyptrae tend to be lacinate rather than strongly ciliate at base. The significance of their different geographic distributions is minimized by the occurrence of *O. subulatum* in Asia and South America.

Globose propagula clustered in the leaf axils are also a feature of *O. sessile*, but the two species do not appear closely related. *Ochrobryum sessile* has linear leaves, slenderly acute leaf apices and apical ventral leucocysts that are uni- or bi-layered for only a single cell width.

3. *Ochrobryum sakalavum* Card. & Par. in Card., Bull. Herb. Boissier, Sér. 2, 4: 99. 1904. TYPE. MADAGASCAR. Territoire Sakalave: cercle de Maintirano, secteur de Rakobe, poste d'ampoza, près du village de Tahutofoly, sur bois pourri; récolté par un tirailleur sakalave (PC).

Ochrobryum sakalavum Card. & Par. in Par., Rev. Bryol. 29. 1902, nom. nud.

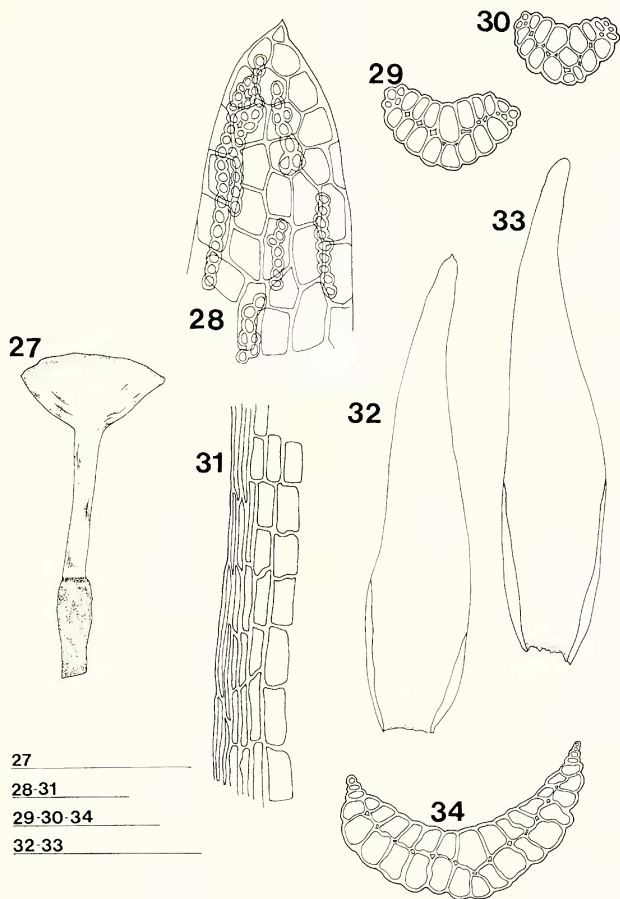
Plants in compact tufts, yellowish-white. Stems 5 mm high. Leaves 2–4 mm long, 0.3–0.4 mm broad, closely erect-patent or subflexuose, narrowly ovate-lanceolate, shortly acuminate, obtuse to subacute and apiculate, not particularly swollen or fleshy at the apex; margins erect; leaf lamina narrow, consisting of 2–4 rows of elongate-rectangular cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; apical ventral leucocysts in two layers for single cell width at the middle of the leaf. Asexual propagula not seen. Setae smooth, 1.2 mm long (with vaginula); capsules immersed, 0.3–0.5 mm long; operculum and calyptra not seen. [Cardot (1904): operculum convex-conical to 1 mm, calyptra long subulate, fimbriate at base, 2.5–2.75 mm long.]

Distribution. Madagascar.

Illustrations. Renault and Cardot (1915, pl. 155, figs. 2a–2s); Figs. 27–34.

Habitat. On rotting wood.

Specimen examined. MADAGASCAR. Territoire Sakalave: cercle de Maintirano, without collector or number (PC).



FIGS. 27-34. *Ochrobryum sakalavum*. 27. Capsule, seta and vaginula. 28. Leaf apex. 29 & 30. Leaf cross section at apex. 31. Basal leaf lamina. 32 & 33. Leaves. 34. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2 = 0.1; 3 = 0.2. All figures from the type.

Ochrobryum sakalavum has narrowly ovate-lanceolate leaves that are commonly obtuse and apiculate above, narrow leaf laminae, and immersed capsules. This species occupies an intermediate position in the genus. The other four species can be divided into two groups: *gardneri*-*kurzianum* and *subulatum*-*sessile*. Its ovate-lanceolate, obtuse, occasionally apiculate leaves are found in the *gardneri*-*kurzianum* group, but unlike that group the leaf apices are not distinctly fleshy and the apical ventral leucocysts are bi-layered only for a single cell width at the very tip of the leaves. These deviate features are found in the *subulatum*-*sessile* group, but that group has longer, linear, sharply acute leaves. It differs from all species of *Ochrobryum* by its relatively narrow leaf laminae that are composed of broader, less attenuate cells. Globose propagula were neither reported by Cardot (1904) nor Renaud and Cardot (1915), nor observed in the only collection available for study. This collection had only a few plants and it was not possible to adequately determine if the species produces propagula.

4. *Ochrobryum sessile* Allen, sp. nov.

Ab *O. gardneri* (C. Müll.) Mitt. cellulis hyalinis distalibus ventralibus saepissime unistratis gemmisque sessilibus in axillis foliorum superiorum differt.

Plants in compact tufts or cushions, dark greenish-white, becoming yellowish-green with age. Stems 3–10 mm high. Leaves 4–5 mm long, 0.2–0.5 mm broad, erect-patent to falcate, narrowly lanceolate, acuminate, ending in a single sharp, hyaline cell, flattened above and commonly spirally twisted when dry; margins erect to incurved below; leaf laminae narrow, consisting of 2–3 rows of long-rectangular, variously porose cells at midleaf and 4–5 rows of elongate-rectangular cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf, apical ventral leucocysts occasionally two-layered for a single cell width. Asexual reproduction by hyaline or brown, multicellular, globose propagula on short or long stalks usually clustered in the axils of the upper leaves, at times also in the lower leaf axils or on slender rhizoids at base of stem. Setae smooth, 1.0–1.5 mm long; capsules immersed to emergent, 0.7–1.0 mm long; opercula 1.5–2.0 mm long. Calyptrae 3–6 mm long, weakly ciliate at base. Spores spherical, lightly papillose, 15–18 μ m.

TYPE. COLOMBIA. Meta: in *Remijia* forest west of Cordillera Oriental. *Steere* 7654 (MO holotype; H, NY isotypes).

Distribution. Central and South America (Costa Rica, Panama, Colombia, and Venezuela).

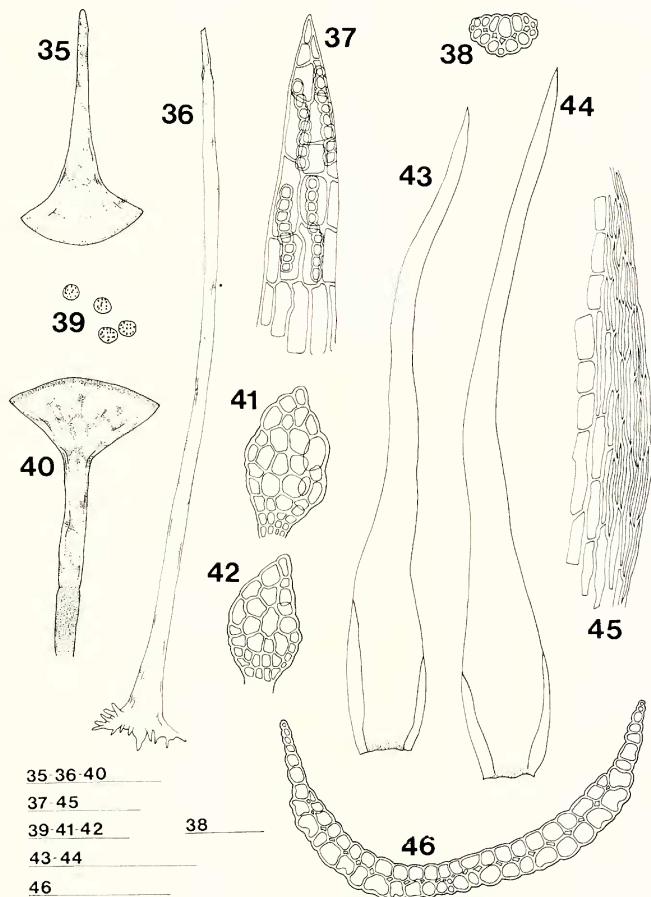
Illustrations. Figs. 35–46.

Habitat. On rotting logs or bark at base of trees; 700–2000 m.

Specimens examined. CENTRAL AMERICA. COSTA RICA. San José: El General. *Skutch* 2209 (FH, MO, US); Puntarenas: 5 km S of S. Vito, *Crosby* 2658 (MO). PANAMA. Darién: Pirre Massif, W of Cana, *Allen* 8849, 8891 (MO, PMA); Panamá: Cerro Azul, *Castillo* 112C (MO).

SOUTH AMERICA. COLOMBIA. Meta: *Remijia* west of Villavicencio. *Steere* 7654 (H, MO, NY). VENEZUELA. Aragua: Parque Nacional Henri Pittier, *Guzmán Ma-761a* (US); Carabobo: between Valencia and Maracay, *Alston* 6152 (BM, FH, US).

This species resembles *O. subulatum* in leaf shape, but is a larger plant that grades into the more narrow-leaved expressions of *O. gardneri*. It differs from *O. subulatum* not only by its larger, more frequently spirally twisted leaves but also by its more strongly papillose spores, and propagula clustered in the leaf axils—a



FIGS. 35–46. *Ochrobryum sessile*. 35. Operculum. 36. Calyptra. 37. Leaf apex. 38. Leaf cross-section at apex. 39. Spores. 40. Capsule, seta and vaginula. 41 & 42. Globose propagula. 43 & 44. Leaves. 45. Basal leaf lamina. 46. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2, 3 & 6 = 0.1; 5 = 0.2. All figures from the type.

feature it shares with *O. kurzianum*. In *O. gardneri* and *O. kurzianum* the leaf tips are thickened, fleshy and have an extensive multi-layered ventral leucocyst pattern. In addition, *O. gardneri* has propagula borne on the upper dorsal surface of the leaves. The leaf tips in *O. sessile* are identical to those of *O. sakalavum* in having the apical ventral leucocysts two-layered for a single cell width at the middle of the leaf. *Ochrobryum sakalavum* has obtuse leaf tips.

5. *Ochrobryum subulatum* Hampe in Besch., J. Bot. (Morot) 11: 150. 1897. TYPE. BURMA. Plumadoc, Kurz 2833 (BM holotype; H, NY isotypes).

Ochrobryum subulatum Hampe in F. Mason, Burma 2: 49. 1883, *nom. nud.*

Ochrobryum stenophyllum Besch., J. Bot. (Morot) 11: 150. 1897. TYPE. BRAZIL. Spruce 73 p.p. (BM holotype; BR isotype; Spruce 73b BM, H isotypes), see nomenclatural note 2, *syn. nov.*

Ochrobryum maclaudii Card. & Par. in Par., Rev. Bryol. 30: 101. 1903. TYPE. GUINEA. Ad ligna semiputrida secus amnem Féfiné, 20 mart. 1903, *Maclaud* (H, NY isotypes), see nomenclatural note 3, *syn. nov.*

Ochrobryum normandii var. *fragilifolium* Dix. & Thér., Rev. Bryol. Lichénol. 12: 69. 1942. TYPE. ZAIRE. Lulua, octob. 1923, *Overlaet* (BM isotype), *syn. nov.*

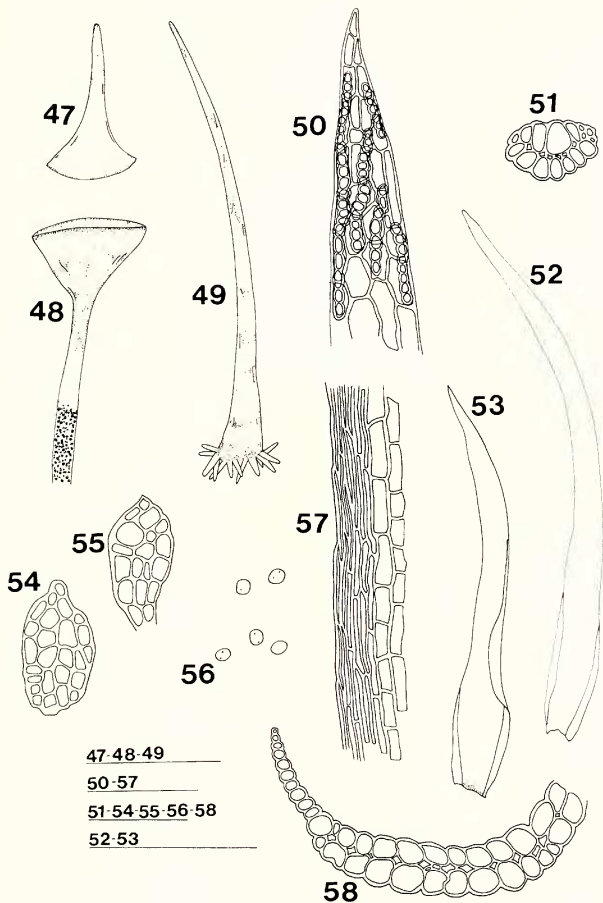
Ochrobryum microphyllum Card. ex Herz., Hedwigia 61: 295. 1919, *nom. illeg.*, see nomenclatural note 4. Based on MALAYSIA. Malakka obes "Batang Padang-Tal", *Stresemann* 86 (H). Non *O. microphyllum* (Besch.) Card.

Ochrobryum herzogianum Mohamed & Tan, Bryologist 91: 29. 1988, *nom. nov.* for *O. microphyllum* Card. ex Herz., *nom. illeg.*

Nomenclatural notes.

1. *Ochrobryum subulatum* and *O. stenophyllum* have equal priority. The epithet *subulatum* was chosen for the combined species because its type material is better.
2. The type of *O. stenophyllum* was separated from a specimen in PC (*Spruce 73*) issued by Spruce in his Musci Amazonici et Andini exsiccati. Previously, *Spruce 73* in BM had been recognized as a mixed collection, divided, and given the numbers *Spruce 73* and *Spruce 73b*. *Spruce 73b* (BM) is identical to the holotype of *O. stenophyllum*. *Spruce 73* (BM) is identical to the holotype of *O. gardneri* var. *microphyllum*.
3. Cardot and Paris failed to cite type material for *Ochrobryum maclaudii*. The type was later designated by Paris (1904).
4. *Ochrobryum microphyllum* Card. ex Herz. was never validly described, furthermore neither Herzog (1919) nor Dixon (1926) intended to describe a new species for this taxon. Likewise *O. herzogianum* is also invalid. The specimen on which the name is based is *O. subulatum*.

Plants slender, in compact or loose tufts. Stems 2–4(–7) mm long. Leaves 2.0–4.5 mm long, erect-patent to secund, linear, evenly tapered from the base to a setaceous or narrowly acuminate apex, not apiculate, but frequently ending in a single, sharp, clear cell; margins erect below; leaf lamina restricted to 5–6 rows of linear or elongate-rectangular cells at basal margins; costa in cross-section with a single ventral leucocyst-layer and a single dorsal leucocyst-layer throughout the leaf. Vegetative reproduction by globose, multicellular propagula arising on short stalks and occurring in terminal clusters on specialized branches or stem extensions; propaguliferous branches to 2 mm long, red-brown, with short, ovate leaves. Setae 1.0 mm long; capsules hemispherical to cupulate, 0.5 mm long; opercula 1.5 mm long. Calyptrae 3–4 mm long, ciliate at base. Spores smooth to lightly roughened, 17–20 μm .



FIGS. 47-58. *Ochrobryum subulatum*. 47. Operculum. 48. Capsule, seta and vaginula. 49. Calyptra. 50. Leaf apex. 51. Leaf cross-section at apex. 52 & 53. Leaves. 54 & 55. Globose propagula. 56. Spores. 57. Basal leaf lamina. 58. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2 & 3 = 0.1. Figs. 47-49, 51, 58 from *Touw 10290*; figs. 50, 52, 53, 57 from *Kurz 2883*; figs. 54-56 from *Fife et al. 4247*.

Distribution. Asia (Burma, Thailand, and Malaysia); South America (Venezuela, Brazil, and Bolivia); Africa (Guinea and Zaire).

Illustrations. Bescherelle (1897, fig. 7); Cardot (1900, pl. 8, figs. 38, 42); Figs. 47–58.

Habitat. On rotting, decorticated logs and on bark at base of trees; 100–1650 m.

Specimens examined. ASIA. BURMA. Plumadoc, *Kurz* 2833 (BM, H, NY). THAILAND. 18°35'N, 98°30'E. *Toww* 10290 (BM, MO, NY). MALAYSIA. Batang Padang-Tal, *Stresemann* 86 (H).

SOUTH AMERICA. VENEZUELA. Bolívar: 4°25'N, 61°20'W. *Steyernark & Dunsterville* 112253 (MO); Mérida: 7°41'N, 71°28'W. *Liesner & González* 9371 (MO). BRAZIL. Acre: 33 km S of Rio Branco along road to Brasília. *Reese & McPherson* 13263 (MO, NY); Alagoas: 33 km N of Macció. *Boom & Mori* 1024 (NY); Goiás: 3 km S of São João de Aliança. *Irwin et al.* 31982 p.p. (FH, H, NY); Mato Grosso: Veu de Noiva, Chapada dos Guimarães. *Prance et al.* 19015, 19016, 19149, 19398 (all NY); Minas Gerais: near Franca. *Wacket* 1171, 1172 (H); Rondônia: 11°S, 64°W. *Reese* 13488 (MO, NY, US), 15 km E of Santa Barbara. *Prance & Ramos* 6910 (FH, NY), 9°10'S, 63°07'W. *Fife et al.* 4247 (MO), 128 km SW of Ariquaeas. *McFarland* 138 (MO, NY). BOLIVIA. Beni: vicinity of Guayaramerín. *Reese* 12910, 13130 (MO, NY).

AFRICA. GUINEA. Koulaire, *Maclaud* (H). Casamonce-Boubounda, *Maclaud* (H), along Féfiné River, *Maclaud* (H, NY). ZAIRE. Lulua, *Overlaet* (BM).

This is the smallest species in the genus and the only one with propagula in terminal clusters on specialized branches or stem extensions. The propaguliferous branches can be recognized, even without propagula, by their terminal position, striking red-brown color and short, ovate leaves.

Ochrobryum subulatum and *O. sessile* form a pair united by their narrow leaves that smoothly taper from base to a setaceous or long-acuminate apex. Unlike *O. kurzianum*, *O. gardneri*, and *O. sakalavum* the apex is not obtuse or apiculate. However, the leaves frequently end in a single, sharp, clear cell, a condition also seen in *O. sessile* and some leaves of *O. gardneri*. *Ochrobryum kurzianum* and *O. gardneri* also have thickened or swollen leaf apices. *Ochrobryum sessile* is a larger plant with falcate leaves that are distinctly twisted when dry. It has propagula clustered in the leaf axils and calyptrae that are weakly ciliate at base.

In South America and Africa *O. subulatum* often occurs mixed with *O. gardneri*. *Ochrobryum gardneri* has larger, stouter leaves, some obtuse, swollen leaf apices, and leaf propagula on the upper dorsal surface of the leaves.

There is a small, sterile *Leucobryum*-like moss in Brazil (*Buck* 2336 NY, 2749 NY, 3081 MO, NY) that closely mimics *O. subulatum* in size and aspect. This taxon also has leaves with a single layer of dorsal and ventral leucocysts. It differs from *O. subulatum* in its virtual absence of a basal leaf lamina, lack of globose propagula and the presence of rectangular chlorocysts in the upper parts of its leaves.

TYPES NOT SEEN

Ochrobryum mittenii C. Müll. ex Besch., *J. Bot. (Morot)* 11: 148. 1897. TYPE. CEYLON, 1862, *Nietner* (in Herb. C. Müll.).

Ochrobryum nietneri C. Müll. ex Besch., *J. Bot. (Morot)* 11: 151. 1897. TYPE. CEYLON, 1862, *Nietner* (in Herb. C. Müll.).

Cardot (1900) provisionally excluded these species from *Ochrobryum* since their sporophytes were unknown. From their descriptions it is not possible to determine if they belong in *Ochrobryum*.

EXCLUDED SPECIES

Leucobryum incurvifolium C. Müll.

Ochrobryum obtusissimum Dix., J. Bot. 76: 225. 1938. TYPES. TANZANIA. Mufindi, *Balbo 96* (BM holotype); NYASALAND [MALAWI]. Bandowe, Chinteché, *Little 2539* (BM paratype), Nchese Mt., *Davy 1312* (BM paratype), *syn. nov.*

The sporophytes of *O. obtusissimum* are unknown, but the presence of multi-layered leucocysts in the leaf bases, quadrate lower laminal cells and masses of brood leaves at the stem apices are features indicative of *Leucobryum* rather than *Ochrobryum*. In these gametophytic features, as well as its leaf shape, cucullate, fleshy leaf apices, and rounded apical chlorocysts it is a perfect match for *Leucobryum incurvifolium*. The inclusion of this taxon in *L. incurvifolium* gives that species a bi-centric distribution: Central America (Mexico to Honduras, see Robinson 1965, and Nicaragua [*Standley 9561*, F, FH])—Africa (Angola [*Gossweiler 11448*, BM], Malawi, Tanzania).

Leucobryum subobtusifolium (Broth.) Allen, *comb. nov.*

Ochrobryum subobtusifolium Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 Afd. 3(7): 10. 1900. TYPE. BRAZIL. Mato Grosso: Serra da Chapada, *Lindman 402* (H holotype; H isotype).

Ochrobryum parvulum Besch., J. Bot. (Morot) 11: 147. 1897. Non *Leucobryum parvulum* Card. TYPE. BRAZIL. Ad flumen Amazone, *Spruce 73 p.p.* (BR isotype), *syn. nov.*

Ochrobryum gardneri var. *microphyllum* Besch., J. Bot. (Morot) 11: 142. 1897. *Ochrobryum microphyllum* (Besch.) Card., Mém. Soc. Sci. Nat. Cherbourg 32: 28. 1900. TYPE. BRAZIL. Sur les troncs d'arbres le long du fleuve Amazone, *Spruce 73 p.p.* (BM holotype; BR isotype) *syn. nov.*

The oldest name for this taxon in *Leucobryum* is preoccupied by *L. parvulum* Card. The epithets *subobtusifolium* and *microphyllum* have the same year of priority (both distributed as off-prints at earlier dates than the journals in which they appeared). *Ochrobryum subobtusifolium* appeared sometime between 14 March and 31 December 1900; *O. microphyllum* sometime between 31 May and 31 December 1900. I have not determined the exact dates of issue for these off-prints but have chosen the epithet *subobtusifolium* as the name for the combined species because of its potentially earlier date.

The sporophytes of this species are unknown and so its generic position is uncertain. Unlike *Ochrobryum* it reproduces asexually by means of apical clusters of brood leaves rather than globose propagula. It is similar to *Leucobryum incurvifolium* and like that species and *Ochrobryum* species has short, rounded apical leaf chlorocysts. It differs from *L. incurvifolium* in having its dorsal and ventral leucocysts in a single layer throughout the leaf.

Leucobryum ceylanicum (Besch.) Card., Mém. Soc. Sci. Nat. Cherbourg 32: 15. 1900. *Ochrobryum ceylanicum* Besch., J. Bot. (Morot) 11: 148. 1897. TYPE. CEYLON. *Thwaites 81* (BM holotype; H, NY isotypes).

The sporophytes of this species are unknown. Cardot (1900) transferred it to *Leucobryum* on the basis of its multilayered, basal leucocysts.

Leucobryum humillimum Card., Mém. Soc. Sci. Nat. Cherbourg 32: 15. 1900, *nom. nov. pro Ochrobryum wightii* Besch., J. Bot. (Morot) 11: 149. 1897, non *Leucobryum wightii* Mitt. TYPE. INDIA. Madras, *Wight* (BM holotype; BM, NY isotypes).

Ochrobryum propaguliferum Dix., Notes Roy. Bot. Gard. Edinburgh 19: 281. 1938. *Leucobryum propaguliferum* (Dix.) Robins., Bryologist 68: 91. 1965. TYPE. CEYLON [SRI LANKA]. Hunasgiriyia, *Alston 1895* (BM holotype). PARATYPES. CEYLON [SRI LANKA]. Hatton near Hambantotuoya, *Alston 2607* (BM); *Wight* (E, not seen), *syn. nov.*

Dixon unwittingly suggested the above synonymy by his inclusion of an isotype of *O. wightii* in the protologue of *Ochrobryum propaguliferum*. Robinson (1965) placed *O. propaguliferum* in *Leucobryum* on the basis of its terminal clusters of deciduous leaves. As in *Ochrobryum* this species has a single layer of dorsal and ventral leucocysts throughout the leaf.

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